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Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors

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Abstract

1. Bottom-trawl fisheries are wide-spread and cause mortality of benthic invertebrates, which in turn may lead to a decrease in the availability of prey for target fish species. Exploitation also reduces the abundance of the fish species themselves. Modelling studies have shown that bottom trawling could lead to both increases and decreases in fish production, but so far empirical evidence to test these ideas has been very limited. We hypothesize that the effect of bottom trawling on the food intake and condition of fish depends on how the ratio of prey to consumers changes with increasing fishing pressure.
2. We assessed the impact of bottom trawling on the food availability, condition and stomach contents of three flatfishes and Norway lobster in an area in the Kattegat that is characterized by a steep commercial bottom-trawling gradient due to the establishment of an area closed to all fisheries, but otherwise homogeneous environmental conditions.
3. For plaice, prey biomass initially decreased slower with trawling than the biomass of fish, and as a result the amount of food available per plaice increased before decreasing at trawling frequencies >5 times y^{-1}. This pattern was mirrored in both the condition and stomach contents of plaice, and for Long-rough dab.
4. No effect of trawling on dab prey and condition was found. Conversely, the condition of the main target species Norway lobster increased as its biomass decreased with increased trawling intensities.
5. Together these results support the idea that when the abundance of the prey declines in response to exploitation, the ratio of the prey to consumer biomass will determine whether exploitation will result in an increase or a decrease of the food intake and condition of the predator.

Synthesis and application. Our study indicates that fish production may be maximized by keeping trawling intensities relatively low, although this may negatively affect the economically more important *Nephrops* fishery. The effects of bottom trawls may be mitigated by switching to gears that affect prey availability to a lesser extent, such pots/creels.

Keywords: Otter trawl, ecosystem effects of fishing, Kattegat, Marine protected area, density dependence

Introduction

Demersal fisheries using otter and beam trawls are widespread, and typically use heavy ground ropes and chains to drive fish and shellfish from the seabed into nets. Previous studies have found that physical disturbance by bottom trawling causes reductions in biomass, diversity and the body-size of benthic invertebrates (Hiddink *et al.* 2006; Kaiser *et al.* 2006). These effects differ according to the fishing gear used and the habitat in which it is deployed (Kaiser *et al.* 2006). The changes that arise from fishing disturbance in benthic ecosystems are conservation issues in themselves, but there is also ongoing concern that bottom fishing may impact the demersal fish species that depend on these habitats for food (e.g. cod, haddock and flatfish (Auster & Langton 1999)). Consequently, trawling may cause changes in fish food intake, body condition and therefore yield in chronically trawled areas (Fogarty 2005).

Trawling may affect prey availability either negatively or positively depending on the diet of fish and the intensity of trawling. The biomass of benthic invertebrates and that of large benthic invertebrates in particular, decreases strongly with increasing trawling in most habitats (Hiddink *et al.* 2006). This decrease is therefore likely to result in a reduction in the amount of food available to many benthivorous fish species. However, modelling studies suggest that the removal of competition from large benthic fauna at low levels of bottom trawling may benefit small benthic invertebrates that are a preferred source of food source for some fish species (Hiddink, Rijnsdorp & Piet 2008; van Denderen, van Kooten & Rijnsdorp 2013). Very high intensities of trawling ultimately may also remove the smaller prey species (Hinz, Prieto & Kaiser 2009). Model outputs concluded that the effect of trawling on fish populations was dependent on the vulnerability of prey to trawling, the strength of competition among prey and non-prey organisms, and the extent to which the system was characterized by bottom-up or top-down control (van Denderen, van Kooten & Rijnsdorp 2013). Fishing resulted in higher yields and increased persistence when the preferred benthic prey species were more resistant to trawling than less preferred prey. These positive effects occurred in bottom-up controlled scenarios where fish feeding had only limited impact on benthic biomass. By contrast, fishing led to lower yields in all scenarios (top-down and bottom-up controlled systems) when high-quality prey were negatively affected by trawling.

Empirical support for such increases in food availability with trawling remains elusive. Jennings *et al.* (2002) found no change in the biomass of small infaunal polychaetes with chronic trawling. In fact, only one empirical study has recorded increases in food supply for fish: a comparison of fish diets between a high- and low-trawling area in Monterey Bay found that the abundance of an opportunistic worm species (a key prey item in the diet of some flatfish species) increased at high levels of trawling (Engel & Kvitek, 1998). Several studies show that commercial fish species such as dab *Limanda limanda* L. and Norway lobster *Nephrops norvegicus* L. scavenge on animals that were damaged by a trawl pass (Bergmann *et al.* 2002), but such short-term food subsidies by trawling are small relative to the long-term effects of trawling on prey availability (Kaiser & Hiddink 2007).

The indirect effects of trawling through changes in food availability occur at the same time as the direct removal of fish biomass that would occur with any fishing gear (Fogarty 2005), although the mobility of fish means that local changes in consumer abundance do not necessarily persist. Changes in prey abundance are more likely to have a negative effect on the food intake of fish if the amount of available prey per fish also declines. Figure 1 illustrates how different shapes of the relationship between prey and fish biomass and trawling frequency can cause different responses in the prey to fish biomass ratios (i.e. the amount of food available per fish). Subtle differences in the shape of the curve can result in the effect of trawling on the food/fish ratio changing from a declining relationship (e.g. Figure 1c, i and p) to an optimum curve (Figure 1a, e and f). If the fish decline more than their prey the food/fish ratio will go up with increasing levels of fishing.

Empirical studies that have examined the effect of trawling on both benthic prey and the fish simultaneously are scarce. Lloret *et al.* (2007) found that polychaete prey biomass and abundance was lowest in trawled areas and that red mullet, *Mullus barbatus* L., from these areas had lower lipid reserves. Similarly, the condition of the flatfish plaice *Pleuronectes platessa* L., was negatively related to trawling frequency in the Irish Sea. Plaice in this area were able to maintain their stomach fullness despite the reduction of prey biomass, and the reduced body condition was best explained by the additional energetic costs of searching at reduced prey densities (Hiddink *et al.* 2011; Johnson *et al.* 2015). Similarly Shephard, Brophy and Reid (2010) in the Celtic Sea

observed declines in the length-at-age of plaice with increasing trawling over gravel but not over sand.

Here we assessed the effect of bottom trawling on the food availability of fish by simultaneously measuring the abundance of prey, the food intake by fish, the resulting condition of fish and the abundance of fish in an area that had a steep gradient of commercial bottom trawling due to the presence of a permanently closed area, across an otherwise homogeneous environment in the Kattegat. This is one of the first studies that has measured all these parameters simultaneously (see Link *et al.* 2005), and is therefore able to explore how both changes in prey availability and fish abundance with trawling interact to cause changes in fish food intake and condition. Similar previous work often has not been able to detect the potential increases in prey abundance at low levels of trawling because too few areas with low trawling were available for sampling. The selected study area allowed us to overcome this limitation by sampling within and outside areas where trawling has been restricted while controlling for potential confounding variables.

The main objective of this study was to disentangle the effects of changes in prey availability that arise from trawling from the direct effects of trawling and from changes in competition over food sources that can be caused by concomitant changes in the fish population. Bottom trawling is likely to result in local and population level reductions in benthic prey availability, and population level reductions of fish. Because fish are mobile, the local removal of fish by trawling does not necessarily result in longer term reduction in abundance at a local scale because fish are mobile. We hypothesize that food intake and the resulting condition of benthivorous fish relates positively to the biomass of their prey and negatively to the biomass of competitors of benthivorous species (i.e. growth is density-dependent). As prey biomass is expected to decrease with increasing bottom trawling, but consumer biomass may show a variety of responses, the effect on the food availability per fish will depend on which the ratio of those variables. Fish condition could therefore either increase or decrease with increasing trawling intensity.

Methods

We studied three species of benthivorous flatfish (plaice *Pleuronectes platessa,* dab *Limanda limanda,* Long-rough dab *Hippoglossoides platessoides* (Fabricius, 1780)) and Norway lobster *Nephrops norvegicus*. *Nephrops* was the main target species in the commercial fishery in the southern Kattegat and is fished at around MSY. Plaice are also targeted and the stock has been increasing. Dab and Long-rough dab are not commercially targeted in the area and usually discarded when caught. Plaice feed primarily on polychaetes and bivalves (Rijnsdorp & Vingerhoed 2001). Dab feeds on crustaceans, polychaetes, fish, mollusc siphons and (the arms of) brittle stars (Duineveld & Van Noort 1986). Long-rough dab feeds on shrimps, brittle stars and polychaetes (Amezcua, Nash & Veale 2003). Norway lobster feed on a great diversity of prey, including crustaceans, molluscs, polychaetes, echinoderms and fish (Cristo & Cartes 1998).

Outline of sampling procedure

The effects of chronic trawling on the weight-at-length of fish and Norway lobster (together called 'fish' in this paper) was investigated over a muddy fishing ground and associated closed areas in the southern Kattegat (Figure 2) in August 2013. Weight-at-length has been shown to be a proxy for fitness in plaice (Kennedy *et al.* 2008), and although such information is not available for the other species, it does not seem unreasonable to assume that such correlations also exist for these species. *Nephrops* condition is also likely to depend on their moult stage, with a newly moulted animals likely to be light (Eriksson 2006). Three different types of closed areas with different restrictions were created in the Kattegat in 2008 to protect the depleted cod stock, and these management measures resulted in a gradient in trawling effort (Vinther & Eero 2013). The area was divided into a permanently closed area (No-take-zone), a seasonally selective closed area where gears that do not target cod are allowed after the first quarter, and a seasonally closed area (Figure 2). Outside these areas in the Kattegat fishing continues under regular TAC and effort management. The management regime had been in place for 5 years when we sampled the area. Infaunal benthic invertebrates were sampled using a grab while a trawl was used to sample fish and Norway lobsters. Permission to sample inside the closed areas was obtained from the Swedish Agency for Marine and Water Management.

Station selection

We selected 19 sampling stations over muddy ground, between 25 and 40m depth and covering a large range of fishing pressure with stations in all different types of closed areas (No take zone: 6 stations, Seasonal selective closure: 7 stations, Seasonal closure: 3 stations, Open area: 3 stations). Each station was defined as a box of 3x3 km. We reviewed station characteristics after the survey with the most up to date fishing pressure estimates and actual sediment composition information collected during the survey in order to exclude stations that were outliers in terms of sediment composition, depth and fishing pressure and thereby aimed to avoid any confounding effects due to strong deviation in these variables. To identify outliers we used Multi-Dimensional Scaling (MDS) after normalizing the different variables (see Results).

Fishing pressure estimates

Fishing pressure was estimated using European Community Satellite Vessel Monitoring System (VMS) data. The yearly area (km^2) swept by a fishing gear was estimated for each station for a three and half year period, from January 2010 to August 2013. These fishing pressures were estimated at each of the 19 stations by computing the accumulated swept areas within a year from all the bottom-contact fishing gears (otter and bottom pair trawls) by Danish and Swedish vessels larger than 15 m. We assume that the fishing effort of vessels <15m and other countries was small and has the same spatial distribution as that of vessels >15m. We used Danish and Swedish official catch and effort statistics to combine VMS data with logbook data, together with estimates regarding the dimensions of the different gears. The relationships between gear dimensions and vessel size (trawl door spread and vessel engine power) for different métiers (combinations of gear types and target species) were used to define the bottom contact to each logbook trip, and the extended logbook data were combined with interpolated vessel tracks based on VMS data (Hintzen *et al.* 2012). Vessel size information and gear specifications was collected in a pan-European industry-based questionnaire survey (Eigaard *et al.* 2015). This study enabled statistical modelling of the vessel size or vessel engine power ~ gear size relationships for different métiers to be conducted and deduce the width of the seabed swept for each of the (VMS interpolated) fishing events that occurred across the stations. Trawling intensity is expressed here as the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of each station, $9km^2$).

Sampling of fish and invertebrate populations

Fish and invertebrates were sampled using RV Skagerrak. Two tows of 30 min were carried out at each station with an otter trawl (distance across mouth of the net 25 m, 80 mm diamond mesh cod-end) at a speed of 3 knots between 07.45h and 17.00h. The total catch number and weight per species was measured. The length (to the nearest mm) and weight (to the nearest g) of the individual fish in the catch was recorded. If the catch of a species in a haul was large (>50 individuals), a subsample of ≥50 fish was measured and weighed. For *Nephrops*, the carapace length and the total weight was measured. Soft-shelled animals, males with missing limbs and all females (because of a smaller claw size) were excluded from further analysis to reduce variation in condition estimates. Benthic invertebrates were sampled by taking five 0.1 m^2 Smith-McIntyre grabs at haphazard locations within the station box. For each grab, a 50ml sediment sample was retained for grain size analysis and the rest of the sample was sorted over a 1 mm sieve and preserved in 4% formalin for identification. All invertebrates were identified to the highest practicable taxonomic resolution (mostly genus or family) and the wet weight of each individual organism was estimated after blotting. Particle size distributions were determined using a Malvern laser diffraction particle sizer (Blott & Pye 2001).

Fish condition

The condition of individual fish was estimated as the weight-at-length of the fish. In the rest of this paper we will use 'condition' as a synonym of 'weight-at-length'. We used total fish weight for this condition proxy rather than eviscerated weight as higher numbers of fish could be processed that way. Using total weight implies that differences in gonad and stomach content weight between stations may have increased the variation in the condition. The 5% shortest and longest fish per species were excluded from all analyses to avoid biases that could be caused by particularly large or small fish. Only stations where more than 10 fish were caught were used for condition estimates to avoid biased condition estimates due to low numbers of fish; 2 stations were excluded for plaice.

Stomach contents

Plaice and dab of body length 182–299 mm and 168–274 mm, respectively, were selected for stomach-contents analysis. These size ranges minimized the likelihood of incorporating ontogenetic changes in diet. Stomachs of up to 20 individuals of each species per station were extracted and stored in 8% buffered formalin. Prey items were identified to the highest taxonomic resolution possible, counted, weighed and measured. In total, 200 plaice and 295 dab stomachs were analysed. The fraction of empty stomachs was reported separately; other analyses within this study only examined stomachs that had some contents to avoid including fish that had regurgitated their stomach contents. To investigate differences in energy content of the prey species consumed, the mean energy content per stomach was calculated using biomass conversion factors (Brey 2015). The level of stomach fullness of plaice and dab at each site was calculated as the mean stomach content weight as a percentage of body biomass. Stomach contents of Long-rough dab and Norway lobster were not examined.

Analyses

Because we were interested in understanding whether bottom trawling can result in decreases, increases or humped responses in prey availabilities, stomach contents and fish condition, we analysed most data using Generalized Additive Models (GAM) as these allow any shape of relationship to be fitted. To account for the non-independence of fish condition measurements within a station (because many individual fish were measured within a station), the effect of trawling or benthic production on the $\log_{10}$(weight) at $\log_{10}$(length) of fish was estimated using GAMM from the package *mgcv* in R (Wood 2015; Zuur *et al.* 2009), using $\log_{10}$(length) and trawling as fixed factors and using 'Station' as a grouping variable and a Gaussian error distribution. As the interaction between $\log_{10}$(length) and trawling was not significant, this term was excluded from subsequent analyses. Homogeneity of residuals was established through visual examination of plotted standardized residuals versus fitted values.

Results

Environmental conditions

Particle size analysis and subsequent MDS indicated that four stations (K, O, Q and S) were less muddy than the other stations in combination with a high trawling intensity

(see Table S1 in Supporting Information, Figure 3). To avoid confounding of sediment composition with trawling intensity these stations were excluded from further analyses. The trawling intensity on the remaining stations ranged from 0.2 to 7.9 y^{-1}. Some bottom trawling was recorded even in areas that were closed to all trawling.

Infauna

The community of infaunal invertebrates was dominated by brittlestars of the genus *Amphiura* (Forbes, 1843) in terms of abundance and by the ocean quahog *Arctica islandica* L. and heart urchins Spatangoida in terms of biomass. Together these three species comprised 92% of all invertebrate biomass. Mean total community biomass was not significantly related to trawling intensity (Figure 4a, Table 1a), but trawl intensity limited the total biomass that could be found at a station (90% quantile regression, P = 0.029). This pattern can be explained by the influence of the presence of low-density but high-biomass species such as *Arctica* and heart urchins. *Arctica* is long-lived with sporadic recruitment and particularly vulnerable to trawling activities (Witbaard & Bergman 2003). Heart urchins are a large but common species, however, their low density as adults in comparison to other macrofauna, means that that they may not be present in 5 x 0.1m^2 grabs even when they were present at station. As a result, both high and lower total biomasses may be encountered even in low trawling intensity stations while at high trawling stations high biomass were not found. Removing these two species considerably weakened the effect of trawling on overall benthic biomass (90% quantile regression, P = 0.26).

The results of the stomach-contents analysis were used to identify the local prey size-spectrum and calculate from this prey availability for different predator species at different levels of trawling intensities. A comparison of the weight distribution of the infauna and the stomach contents indicated that plaice and dab preferentially selected small infauna as prey (Figure S1); 97.5% of plaice prey was <0.20g, while 97.5% of dab prey was <0.63g and these thresholds were therefore used to define the prey spectrum of these two predators (further stomach contents description are given in the 'Stomach contents' section). When only the size classes that form the food for plaice and dab were considered, *Amphiura* was dominant; 76% of community biomass in the grabs <0.20 g (plaice prey) consisted of *Amphiura* and 84% of community biomass <0.63g (dab prey) consisted of *Amphiura*. Other species in the prey size classes were

mostly polychaetes and bivalves. The biomass of the infauna preyed upon by plaice declined slowly at low trawling frequencies, but faster at trawling frequencies above 5 y^{-1} (Figure 4b, Table 1a). There was no significant relationship between dab prey biomass and trawling intensity (Figure 4c, Table 1a). For Long-rough dab and *Nephrops*, prey availability could not be calculated as no stomach samples were taken for these two species.

Fish and *Nephrops* biomass

Most fish that were caught were c. 20 cm in length, while *Nephrops* was large and had a carapace length of c. 5 cm (Table S2). Dab and *Nephrops* biomass was about five times higher than those of plaice and Long-rough dab (Figure 5). There was a sharp decline in the biomass of dab and *Nephrops* as trawling intensity increased, but this decline levelled off at a trawling intensity of 5 y^{-1} (Figure 5, Table 1b). The biomass of plaice and Long-rough dab did not change with trawling intensity (Figure 5, Table 1b). These four species comprised 89% of the catch biomass in the study area.

Fish condition

Weigh-at-length peaked at a trawling intensity of c. 5 times y^{-1} for both plaice and Long-rough dab (Figure 6, Table 1c). Weight-at-length for dab did not respond to trawling, while *Nephrops* weight-at-length increased with increasing fishing intensity (Figure 6, Table 1c). The difference between the highest and lowest condition recorded was approximately 4% for plaice, Long-rough dab and *Nephrops*.

Figure 6a and b also gives the 'prey to consumer biomass ratio' for plaice and dab for comparison with the fish condition. This ratio was calculated by fitting a GAM through the prey-biomass to fish-biomass ratios (Figure 4b and c divided by Figure 5e). We used total biomass of the three flatfish species plus *Nephrops* as the measure of the abundance of consumers because, in particular, plaice abundance was low in comparison with the abundance of competitors, and therefore the abundance of all species, including plaice, was considered a better proxy for the abundance of competitors than the abundance of plaice alone. The 'plaice-prey to consumer-biomass ratio' peaked at intermediate trawling intensities and showed a similar pattern to the weight-at-length for plaice. The 'dab-prey to consumer-biomass ratio' increased and also showed a similar pattern to (the non-significant) weight-at-length for dab. These

comparable patterns therefore suggest that the ratio of prey-availability to competitor-biomass affects the food intake by these fish and their resulting condition.

Stomach contents

Overall, dab stomachs were much fuller than plaice stomachs. The most common prey item in the stomach of both species was the brittlestar *Amphiura* spp., but the rest of the diet was comprised of mainly polychaetes and bivalves for plaice and crustaceans for dab (Figure S2). Even though *Amphiura* has a low energy density (Table S3), it still contributed most of the energy in the diet of both species at most stations. The percentage of empty stomachs did not respond to trawling in either of the two species (Figure 7a-b, Table 1d). Stomach fullness and the stomach energy content approximately doubled across the trawling gradient for plaice, but did not change with trawling for dab (Figure 7c-f, Table 1d).

Discussion

The results from this study support our hypothesis that food intake and the resulting condition of some benthivorous fish is affected by both competitor abundance and prey availability and relates positively to the biomass of their prey and negatively to the biomass of competitors. The effects of trawling on fish condition were modest (around a 4% increase across the trawling gradient for plaice, Long-rough dab and *Nephrops* relative to an untrawled situation). For plaice, prey biomass initially decreased more slowly than the biomass of consumers, and as a result the amount of food available per individual plaice increased initially before decreasing at higher trawling frequencies. This pattern was mirrored in both the condition and stomach contents of plaice, which both peaked at intermediate levels of trawling intensity. No significant effect of trawling on abundance of the preferred prey of dab was detected, and as fish biomass decline the prey/consumer ratio increased moderately for dab. Although not significant, again this pattern was mirrored in both the condition and stomach contents of dab, which both showed increases with increasing trawl intensity. No diet information was available for Long-rough dab, but body condition changed with trawling intensity in a similar way to plaice, which suggests that these two species may rely on a similar diet. *Nephrops* condition increased linearly with increasing trawling, suggesting that their food resources were not strongly affected by trawling, and that a release from competition was the overriding factor driving the increase in body condition for

Nephrops. In addition, scavenging on animals that were damaged by trawling (Bergmann *et al.* 2002) may provide more of a food source at higher fishing intensities. Together these results support the idea that when the abundance of both the prey and the target predator are affected by exploitation, it is important to know how the ratio of these changes as this will determine whether exploitation will result in an increase or a decrease of the food intake, condition and growth rates of the target species. Our results show that the assumption of Van Denderen *et al.* (2013) that prey abundance will increase with trawling was not supported, but our results do confirm that it is important to take into account the top-down effects of fish predation on benthic prey when trying to assess the effect of bottom trawling on fish productivity.

Foraging in areas where prey abundance is low is more energetically costly than foraging in areas where prey is more abundant due to the increased search time (Croy & Hughes 1991). If this increase in energy expenditure at low prey abundance is substantial, it could be expected that the effect of trawling on fish condition is stronger than the effect on stomach contents; fish may still fill their stomach at low prey abundance but need to expend more energy to do so. However, such a stronger effect of trawling on condition than on stomach contents was not evident from our results.

The results for plaice are different from the outcomes of a similar study in the Irish Sea, which found that trawling had a monotone negative effect on the condition of plaice (Hiddink *et al.* 2011), explained by dietary shifts in plaice towards energy-poor prey together with a potential decrease in foraging efficiency due to low prey densities (Johnson *et al.* 2015). However, the pattern in the condition of plaice seen in the Irish Sea (Hiddink *et al.* 2011) does follow the prey/predator ratio; both prey and fish abundance show a logarithmic decline with trawling but fish abundance declined more slowly and therefore the prey/predator ratio declined. Therefore, although a different response of plaice condition to trawling was recorded in this previous study, the mechanisms explaining the response are the same. This indicates that the response of fish food intake to bottom trawling may vary from one location to another according the conditions, and abundance of competitors.

An important assumption was that consumers compete for food and that growth was density-dependent. In a laboratory study the weight of a standard-length plaice of

247mm (Figure 6a) decreased from 157g after unlimited feeding to 143g after a month of starvation (Fonds *et al.* 1992). The best-condition plaice in our study had a similar weight to the well-fed laboratory fish, while the worst condition plaice in the Kattegat had a condition similar to starved fish (Figure 6). This suggests that the variation in plaice condition in the Kattegat indeed represents substantial differences in food availability. Another important assumption was that the different consumers at least partly share the same prey. Given the dominance of *Amphiura* in the environment, and in the stomachs of plaice and dab, this does not seem an unreasonable assumption. *Nephrops* was the most abundant species in the catch, and is likely to be undersampled because we fished during daylight hours when these animals tend to hide in their burrows. Because of the 80 mm mesh of the trawl, only 5% of *Nephrops* numbers were below the minimum landing size of 40 mm carapace length (Table S2), while it can be expected a large fraction of the population is too small to be retained in the net. It is therefore likely that *Nephrops* were considerably more abundant than all the flatfish species together. This means that even a limited prey overlap with flatfish may have made *Nephrops* an important competitor for the flatfish.

Any study using an observational approach has to consider the potential for confounding factors affecting conclusions. This study assumed that the condition of fish represented the local prey availability. Previous work suggests that flatfish forage within quite limited areas (de Castro *et al.* 2015). Contrary to the sessile *Nephrops*, the mobility of the fish in the study area is poorly known, and therefore, we cannot be sure that individuals captured at different stations had been feeding at that station in the time that they built up their condition (weeks) before sampling. This, however, does not affect the conclusions that trawling had an effect on the condition of three of the species, as mobility would break up any spatial pattern in condition; therefore, these analyses are likely to underestimate any effect of trawling on condition. This is confirmed by comparing the magnitude of the effect of trawling on condition with the effect on stomachs contents; the effect on condition was much smaller than the effect on the stomachs. As the stomach contents reflect the food intake in the previous 24h and the condition the previous weeks, this confirms that fish mobility weakens the observed effects.

A problem of using weight-at-length as an indicator of food intake is that as food intake increases, both length and weight may increase which means that a higher food intake will not be reflected in a straightforward increase in length-at-weight (Lloret, Shulman & Love 2014). The length ranges of fish in our samples included both juveniles and adults, and juvenile fish are likely to invest more energy into length growth than adults. This effect will therefore have decreased our ability to detect differences in food intake between stations.

Implications

A general assumption in fisheries management is that fish productivity increases with exploitation because of a reduction in competition over food and other resources. Here we show that fish productivity may decline with exploitation because of a decline in prey abundance. Our results show that the assumption of increasing fish productivity with exploitation is reasonable in the Kattegat fishery for *Nephrops* and dab, but not for plaice and Long-rough dab. Although body condition and food intake for these two species increased with trawling intensity up to a frequency of 3 to 5 y^{-1}, there was no indication that bottom trawling had a positive effect on the prey availability for these species (which contradicts some scenarios in van Denderen, van Kooten & Rijnsdorp 2013). Instead, in comparison to fishing gears that have no effects on prey abundance, intense bottom trawling appears to reduce the capacity of the Kattegat ecosystem to underpin the production of plaice and long-rough dab. In the Kattegat, no specific management for plaice and long-rough dab may be needed as both species are relatively low in abundance and long-rough dab is often discarded, especially as reducing trawling intensity may come at the expense of reducing production of the economically more important *Nephrops*. In areas where plaice is an important commercial species, the production of plaice may be maximized by avoiding trawling at high intensities, and keeping effort below the level at which plaice condition is starting to decline. This threshold was around 3-5 trawl passes y^{-1} in the Kattegat, but is fishing gear and system specific and is likely to change according to local factors such as substratum type and primary production. The effects of bottom trawls may be mitigated by switching to gears that affect prey availability to a lesser extent, such as gill nets, long-lines or pots and creels targeting *Nephrops* (Ziegler & Valentinsson 2008), but it seems unlikely that such gears can sustain the demersal fish market alone.

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Additional supporting information is found in the online version of this article.

Table S1. Site characteristics.

Table S2. Size of the fish.

Table S3. Energy density of prey.

Table S3. Number of stomachs analysed.

Figure S1. Prey weight distribution.

Figure S2. Stomach energy content.

Data Accessibility

Infaunal biomass, fish abundance, lengths and weights are available on datadryad.org. Stomach contents are available from DAPSTOM https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/

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Tables

Table 1. Statistical outputs of GAM and GAMM models. Relationship of response variable to trawling frequency (y^{-1}). Res.df are the residuals degrees of freedom. WW = wet weight. A * indicates that the fit of the GAM(M) curve is significantly better than a straight line according to a Wald chi-square test.

a. Biomass of infauna, g WW per 0.1 m^2. GAM

Parameter	n	res.df	F	P
Total infauna WW	15	13	1.176	0.298
Plaice infauna prey <0.20g WW	15	12.4	4.175	0.041*
Dab infauna prey <0.63 g WW	15	13	0.244	0.630

b. Fish biomass per trawl. GAM

Species	n	res.df	F	P
Pleuronectes platessa	15	12.5	0.717	0.494
Limanda limanda	15	12.0	7.049	0.007*
Hippoglossoides platessoides	15	11.9	2.202	0.144
Nephrops norvegicus	15	12.3	7.301	0.007
Total	15	12.2	6.043	0.013

c. Fish condition. GAMM

Species	n	res.df	F	P
Pleuronectes platessa	372	367.9	6.399	0.002*
Limanda limanda	915	912.0	1.201	0.273
Hippoglossoides platessoides	883	878.9	7.143	0.001*
Nephrops norvegicus	471	467.9	5.853	0.014

d. Fish stomach contents. GAM

Species	n	res.df	F	P
Pleuronectes platessa % empty	13	11.0	0.803	0.389
Limanda limanda % empty	15	12.2	1.555	0.247
Pleuronectes platessa fullness	13	8.9	4.849	0.024
Limanda limanda fullness	15	13.0	2.750	0.121
Pleuronectes platessa energy	13	9.3	4.340	0.034
Limanda limanda energy	15	13.0	2.550	0.134

Figures

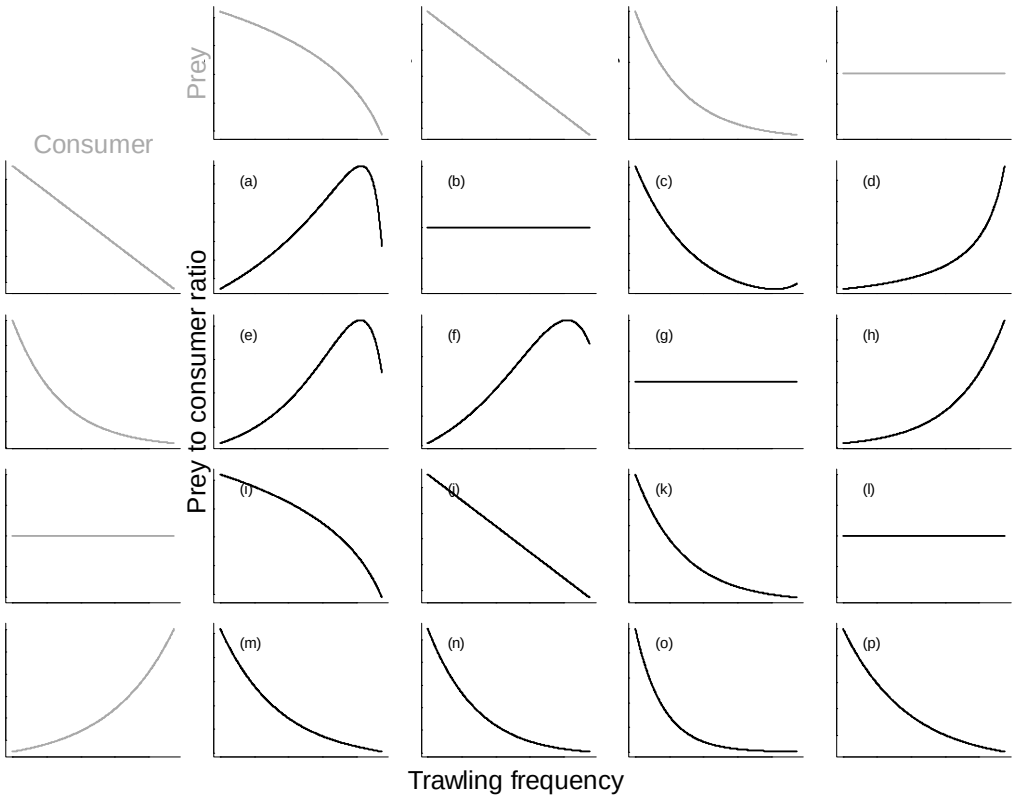


Figure 1. Hypothetical prey to consumer biomass ratios for different shaped relationships between prey (top row) and consumer biomass (left column) and trawling frequency. These relationships reflect the local, rather the population level, effects. Because the prey is not mobile, their local response to trawling is assumed to be neutral or negative. Consumers are mobile and therefore a wide variety of responses is explored, even though the population level response to fishing will be negative.

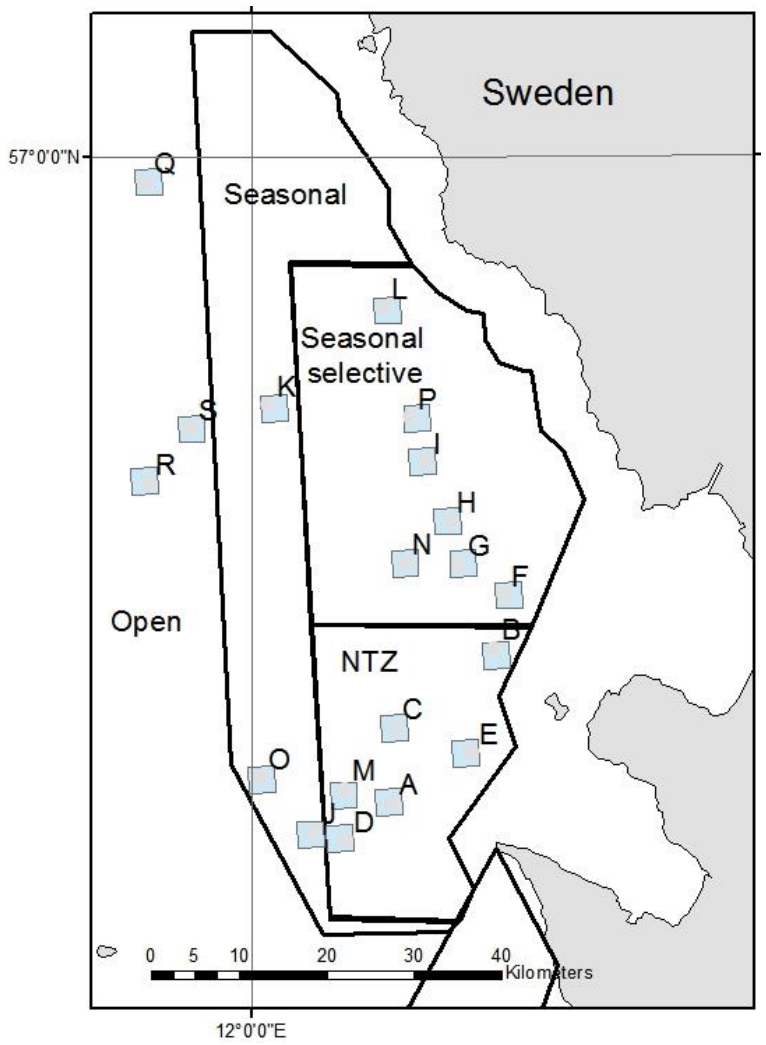
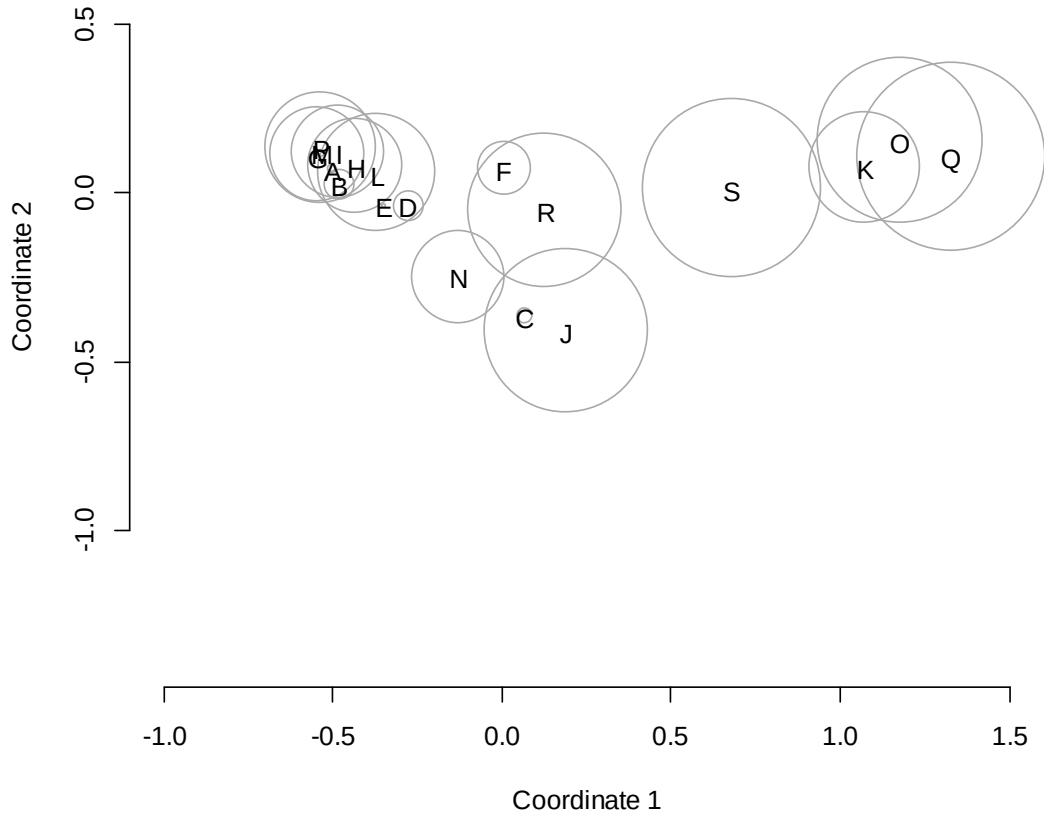


Figure 2. The study area with the sampling stations and management area boundaries. NTZ = No-take zone.



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655 Figure 3. MDS plot of the site characteristics of the sampling stations. Bubble size is

656 proportional to the trawling intensity.

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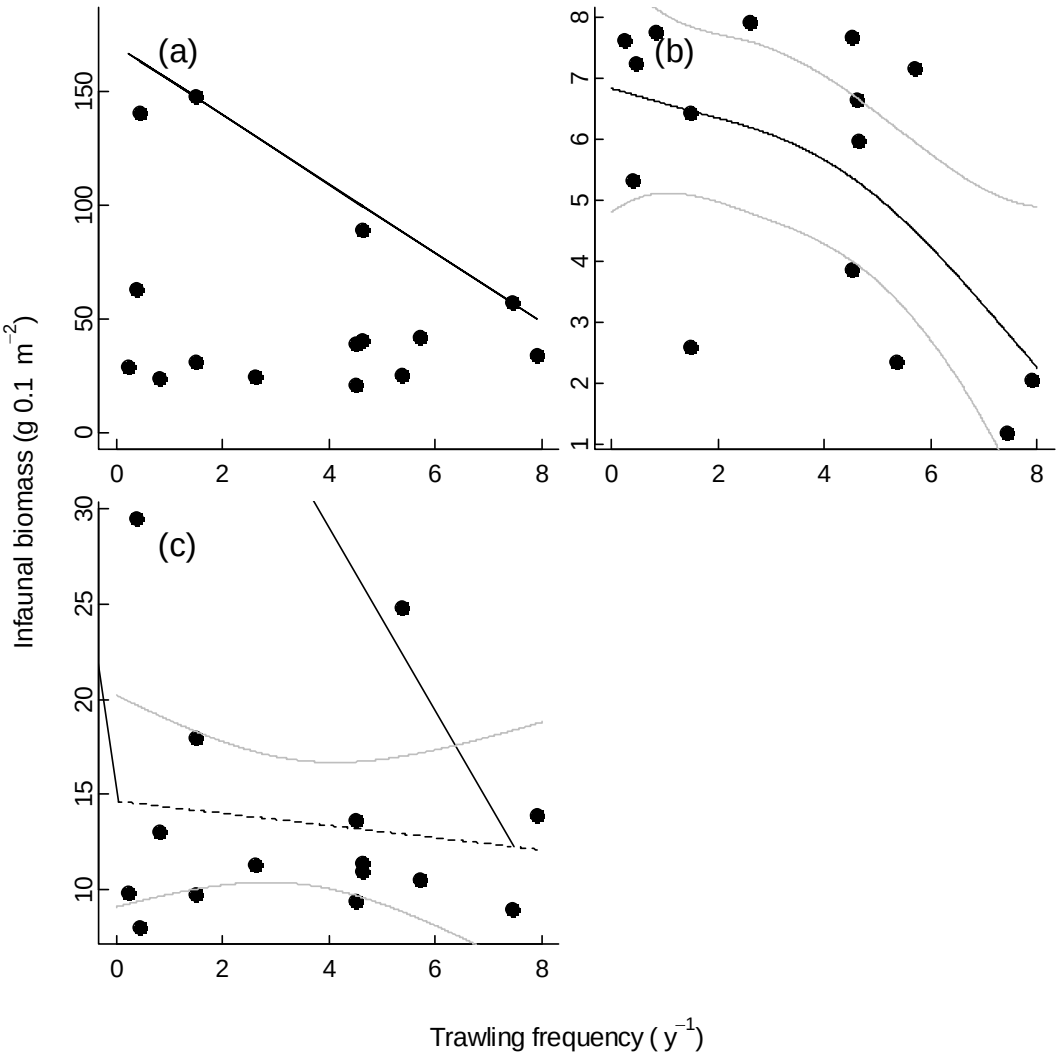


Figure 4. The effect of bottom trawling on the biomass of infaunal benthic invertebrates. a) All infauna, solid line is 90% quantile regression, b) Plaice prey <0.2g, solid line is fitted GAM, Grey lines indicate the 95% confidence interval, c) Dab prey <0.63 g WW. The dashed line is the non-significant GAM for dab.

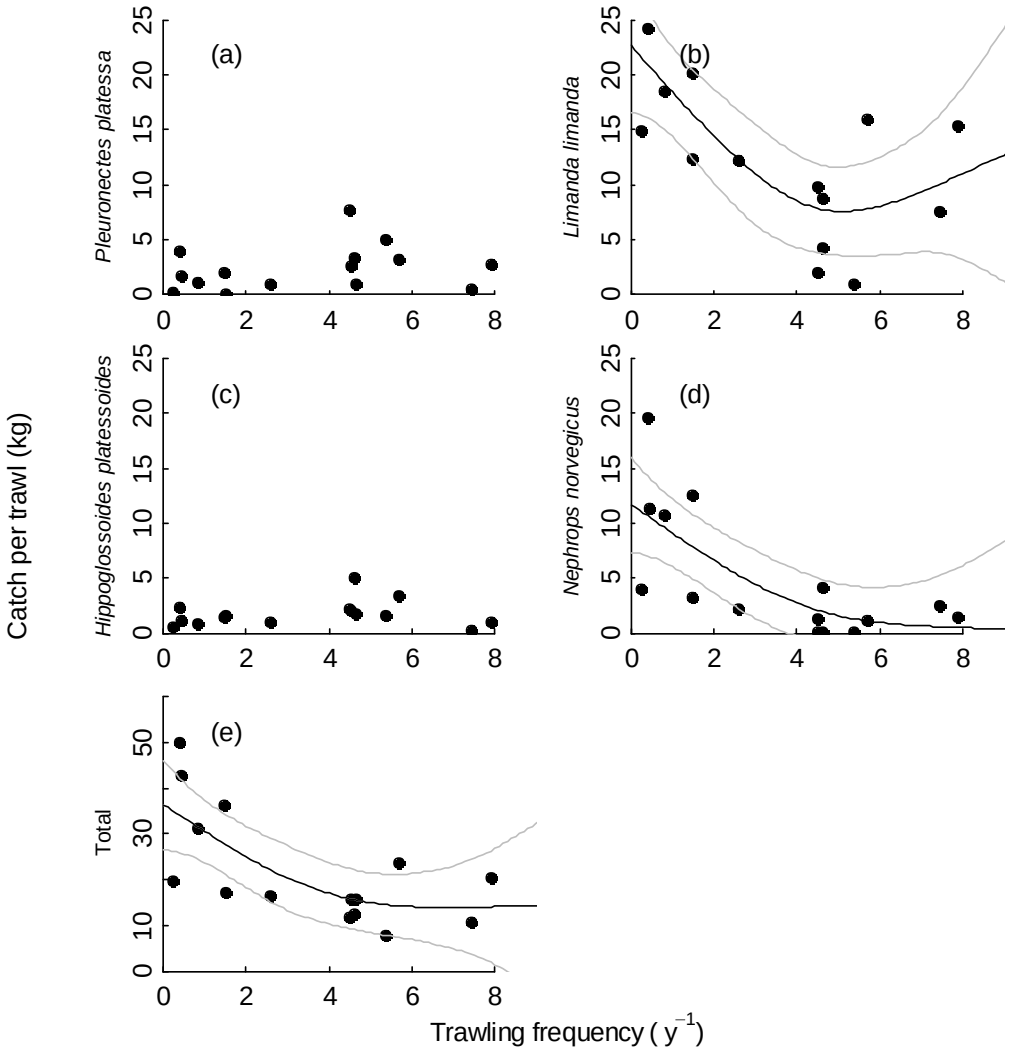
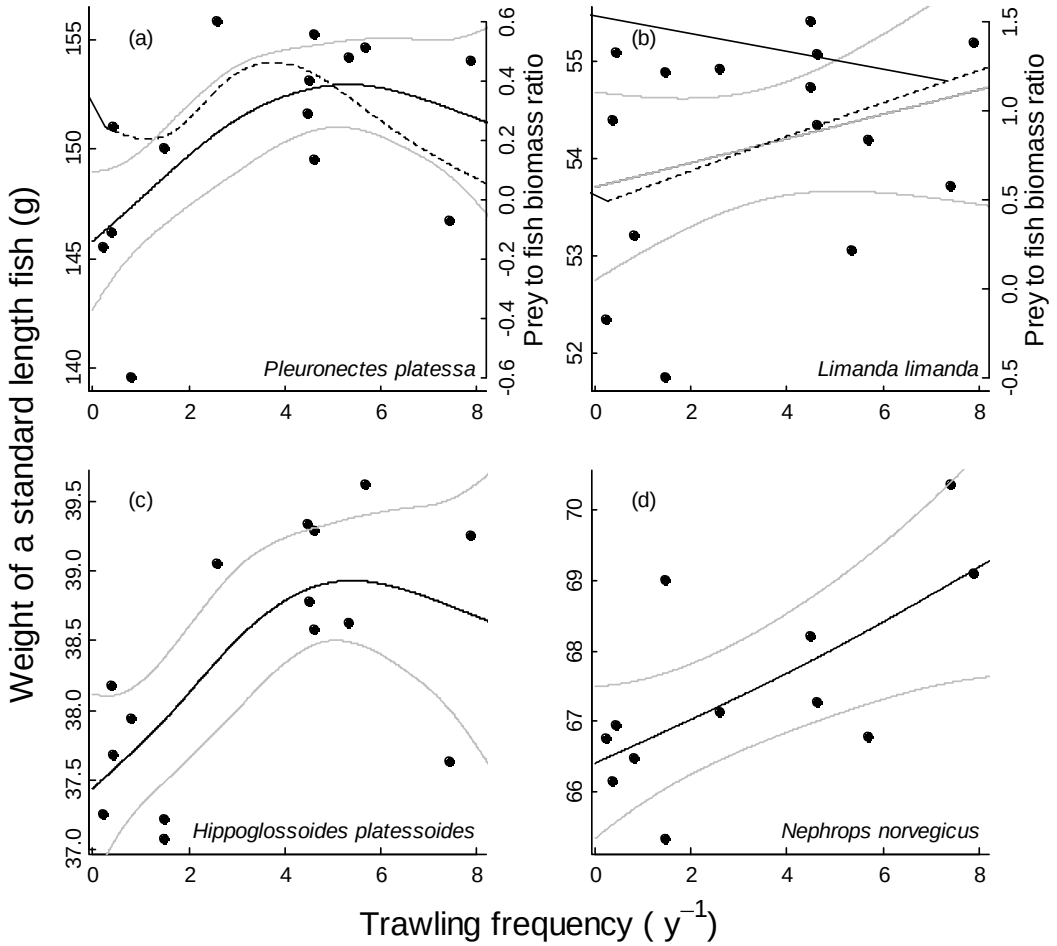


Figure 5. Mean fish biomass per trawl. a) Plaice, b) Dab, c) Long-rough, d) Norway lobster, e) total of all four species. Grey lines indicate the 95% confidence interval.



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671 Figure 6. Weight of a standard length fish (as predicted from the GAMM plus the
672 residuals, solid black line) for a) plaice, b) dab, c) Long-rough dab and c) Norway
673 lobster. The dashed line (right y-axis) is the 'prey to consumer ratio' (g infaunal prey
674 0.1 m^{-2} kg $fish^{-1}$ $trawl^{-1}$) and is given for comparison with the weight-at-length. The
675 GAMM for dab is not significant.

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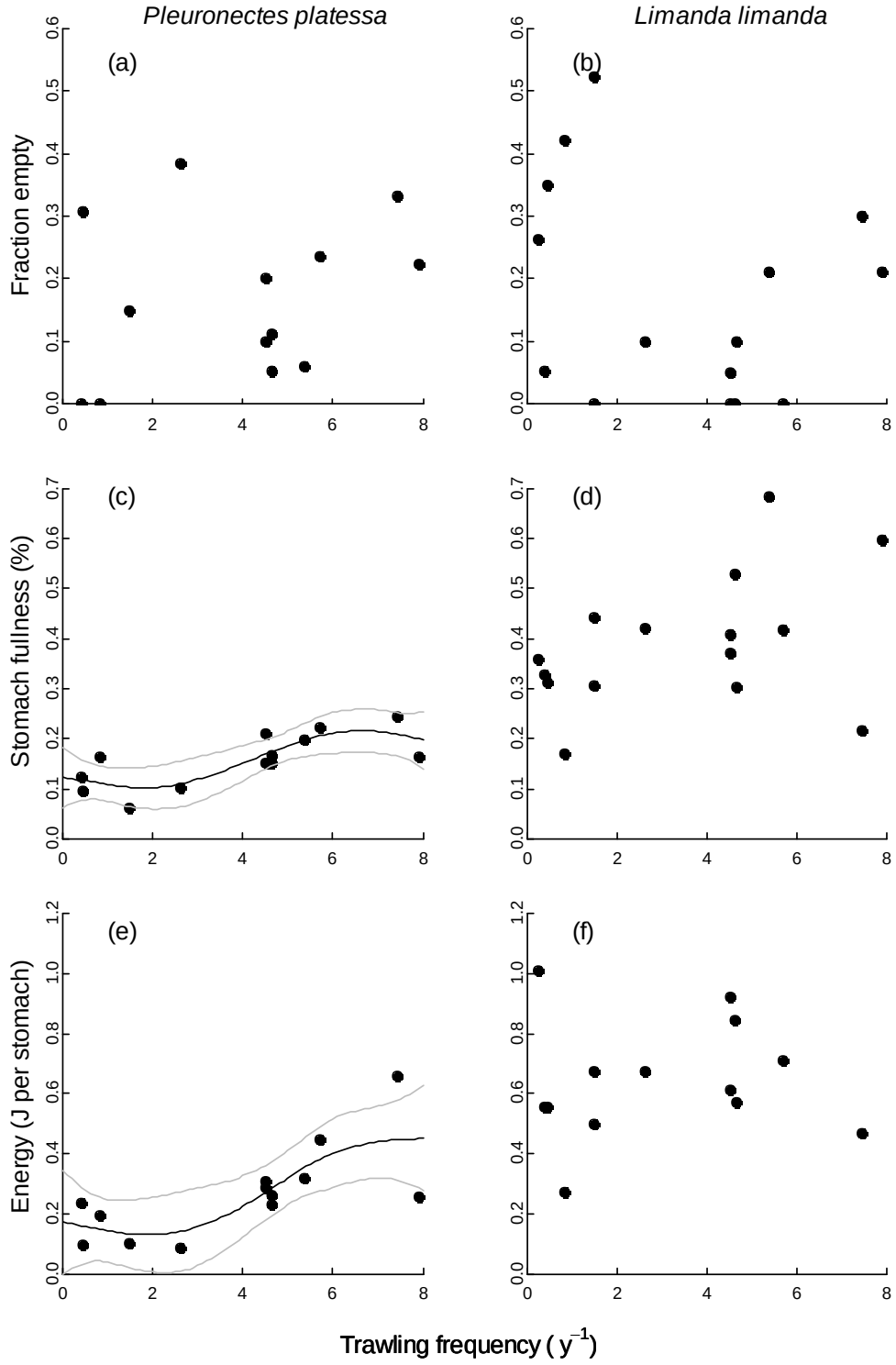

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680 Figure 7. Stomach contents of plaice and dab. a-b: fraction empty, c-d: stomach fullness
681 as a percentage of body weight. e-f: stomach energy content. a, c, e: plaice. b, d, f: dab.

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